Estuaries and Coasts
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Salinity Selection by Juvenile Brown Shrimp (*Farfantepenaeus aztecus*) and White Shrimp (*Litopenaeus setiferus*) in a Gradient Tank

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Abstract Changes in freshwater inflow and salinity patterns may affect the nursery value of estuarine systems for penaeid shrimp, but the relationship between salinity and shrimp abundance is complex and likely confounded by other environmental variables. Laboratory experiments can provide insights into salinity selection, and we designed an experimental gradient tank to examine salinity preferences of juvenile brown shrimp and white shrimp. Our design uses gently flowing water to eliminate various physical constraints often associated with selection experiments. We conducted experiments with juvenile brown shrimp (12 trials) and white shrimp (seven trials), to examine selection for salinities along a gradient from 1 to 42. Data were analyzed using contingency tables and log-linear modeling to examine relationships with salinity and possible interactions with temperature. Both brown shrimp and white shrimp were present in all salinities examined within the experimental range. In general, brown shrimp showed a preference for salinities from 17 to 35 and demonstrated avoidance for the extreme low salinities along the gradient. Results for white shrimp were not statistically significant, and this species did not appear to avoid low salinities. There was no effect of water temperature on the observed selection patterns for brown or white shrimp. Our results suggest that although salinity preferences likely exist for these species, strong distribution trends associated with salinity gradients in estuaries are likely caused by other environmental factors.

Keywords Experimental tank · *Farfantepenaeus aztecus* · *Litopenaeus setiferus* · Log-linear modeling · Penaeid shrimp · Salinity gradient

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Introduction

Alterations to freshwater inflow are increasingly common in coastal estuaries of the Gulf of Mexico. These alterations include both decreases in freshwater due to damming and water removal from upstream in the watershed and increases in freshwater caused by diversions of major rivers, such as the Mississippi, into shallow wetlands. These changes in freshwater inflow can alter salinity patterns in estuaries. Both brown shrimp, *Farfantepenaeus aztecus*, and white shrimp, *Litopenaeus setiferus*, use estuarine systems in the Gulf as nurseries, and juveniles are abundant throughout estuaries for much of the year. Because salinity is a key characteristic of estuarine waters, it has often been considered an important factor in the distribution of shrimp and in determining the nursery value of estuarine habitats (Barrett and Gillespie 1973; Gunter and Hildebrand 1954; Gunter et al. 1964).

The role of salinity in affecting shrimp production appears complex, and salinity preference in estuarine organisms may be a behavioral response allowing them to alter their exposure to adverse conditions (Lockwood 1976; McGaw 2001). Although organism presence and densities in different salinity regimes have been examined as indicators of habitat value and general conclusions have been made regarding the importance of salinity, evidence for effects on the distribution of shrimp in estuaries is contradictory. Both shrimp species have been collected over a wide range of salinities from 0 to 45

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(Practical Salinity Scale), and maximum abundances often occur at intermediate salinities (see Longley 1994 for a review).

Gunter et al. (1964) reported that young brown shrimp in Gulf of Mexico estuaries were most abundant where salinities ranged from 10 to 20, and a summary of trawl data from Texas estuaries suggests that brown shrimp reach their greatest abundance when mean estuarine salinities are between 15 and 25 (Longley 1994). Using enclosure samplers in shallow-water habitats, Zimmerman et al. (1990) found juvenile brown shrimp to be most abundant in the middle and lower reaches of Galveston Bay, TX, where salinities were generally greater than 10. Howe et al. (1999) collected quantitative samples in lower Mobile Bay, AL, and found the highest densities of brown shrimp in salinities from 14 to 19. In a synthesis of published papers and unpublished reports of habitat use in Texas and Louisiana (restricted to quantitative enclosure samples), Minello (1999) reported that young brown shrimp were most abundant in polyhaline and euhaline salinities (i.e., >18). In contrast, Parker (1970) reported that brown shrimp in Galveston Bay were most abundant in salinities less than 5 with abundance decreasing as salinity increased, and Thomas (1999) analyzed trawl data collected in Louisiana and found that the highest abundance of juvenile brown shrimp occurred in salinities less than 10. Shrimp size and gear efficiency may affect these comparisons, but these contradictory results suggest that salinity is just one of the environmental variables affecting field distributions of brown shrimp in estuaries.

White shrimp are generally considered to be at their highest abundances in areas of lower salinity than brown shrimp (Gunter 1961), but the supporting data are inconsistent. Peak abundances of juvenile white shrimp have been reported in estuarine waters with salinities between 0 and 10 in Texas (Gunter et al. 1964) and South Carolina (Wenner and Beatty 1993). Longley (1994), however, summarized several studies in Texas estuaries that showed no effect of salinity on white shrimp distributions, and DeLancey et al. (2008) found similar results in South Carolina. Annual quantitative sampling by Howe et al. (1999) revealed the highest densities of white shrimp in salinities of 7–14 in the lower Mobile Bay estuary. In contrast, Zimmerman et al. (1990) reported highest densities of white shrimp in lower Galveston Bay in association with the highest salinities measured (32), and Minello (1999) summarized enclosure sampler data from Texas and Louisiana estuaries and reported highest mean densities of juvenile white shrimp in polyhaline (salinities from 18 to 30) regions of these systems.

Selection for different salinities can be examined in the laboratory, and such a controlled approach can remove confounding factors and perhaps provide insight into some of the inconsistencies present in field distribution data. A variety of techniques have been developed for this purpose, but most approaches provide relatively few salinity choices, have strong discontinuities between the options, have physical barriers to maintain salinity discontinuities, or have salinity differences confounded with physical tank characteristics (Doudoroff 1938; Hansen 1972; Staaland 1969). Smooth salinity gradients have been developed in vertical chambers by layering water of different densities with high-salinity (high density) water on the bottom and low-salinity water at the top (Hughes 1969). This approach, however, confounds depth or proximity to the bottom of the tank with high salinity. For small organisms that are relatively inactive, Keiser and Aldrich (1973) developed a modification of this approach using a slanted chamber that allowed animals to orient to the bottom at all salinities. Postlarval brown shrimp in the chamber could select for salinities between 0 and 70, and they concentrated at salinities between 5 and 20 (Keiser and Aldrich 1973). Although an improvement over other approaches, this experimental chamber is not ideal for large and more active organisms because they can disrupt the density gradient. Staaland (1969) created a rectangular chamber that was horizontal but used partitions to create a series of discrete salinities. Staaland chambers have been used to determine salinity preference in fishes (Audet et al. 1986; Bos and Thiel 2006; Fivizzani and Spieler 1978; Lankford and Targett 1994; McManus et al. 2014; Miller et al. 1983), and although these studies report that the partitions did not create an obstruction for fish, movement of other organisms could be affected by the tank structure. Other studies have used choice chambers (Benfield and Aldrich 1991, 1992, 1994; James et al. 2008; Keiser and Aldrich 1976; Kroon and Housefield 2003) that generally present experimental animals with only two environmental options. Automated selection systems, which continuously adjust salinity levels in choice chambers in response to changes in animal position, are also useful for examining salinity selection in marine organisms (Serrano et al. 2010).

We designed and constructed a new gradient system to answer the question of whether brown shrimp and white shrimp select for particular salinities when other environmental factors are eliminated. The system presents mobile organisms with a stable salinity gradient in gently flowing water. In this gradient tank, nekton can freely move among areas with salinities as low as 1 and as high as 42. We used the system to examine the salinity preferences of juvenile brown shrimp and white shrimp (30- to 75-mm total length) and to test the null hypothesis that juvenile shrimp of each species will not select for any particular salinity within the experimental range.

Materials and Methods

The gradient chamber was constructed using a circular fiberglass raceway tank with walls 0.60 m in height, an outer diameter of 3.0 m, and an inner diameter of 2.4 m (Figs. 1 and 2). In

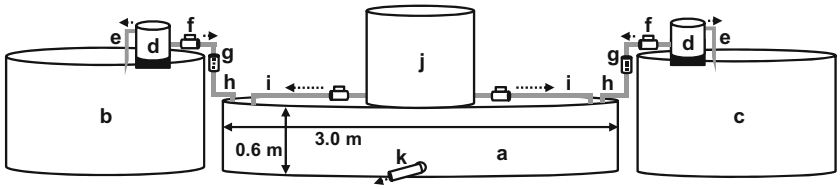

Fig. 1 Schematic representation of the gradient and supply tanks, *side view*: (*a*) gradient tank, (*b*) freshwater supply tank, (*c*) saltwater supply tank, (*d*) head tank, (*e*) overflow pipe, (*f*) ball valve, (*g*) in-line flowmeter, (*h*) water input with spray bar, (*i*) control water input with spray bar, (*j*) control water supply tank, and (*k*) adjustable stand pipe and drain. *Dashed arrows* indicate the direction of water movement

this initial configuration, the circular raceway was 0.30 m wide and 8.5 m long with a maximum volume of 1600 L. We added a 0.60-m tall dividing wall between the interior and exterior walls, creating two separate and independent raceways each measuring 0.15 m wide, and finished all interior surfaces with a neutral tan-colored gel coat. Each raceway had two drains at the base of the walls with 5-cm diameter openings covered with 3-mm mesh installed flush with the tank wall. Drains were located on opposite sides of the tank and were equipped with external adjustable stand pipes to readily manipulate water depth.

The salinity gradient was established in the experimental raceway by introducing freshwater and saltwater (salinity of 45) on opposite sides of the tank between the drain locations. In the control raceway, experimental flow rates were replicated using water with a constant salinity of 20. Supply tanks (maximum capacity of 1800 L) with an elevated 19-L head tank were used to distribute water to the raceways at a steady rate of flow. A small submersible pump in each supply tank continuously circulated water to the head tank, with overflow returned to the supply tank. Water flowed from head tanks into the raceways by gravity, with a ball valve used to manually set flow rates. Flow rates were measured with Gilmont Instruments Unshielded Flowmeters (Barnant Company, Barrington, IL) using stainless steel float balls. Water was introduced into the raceways through spray bars that extended horizontally across the surface of the chambers. Air stones were used to ensure complete vertical mixing throughout the raceways.

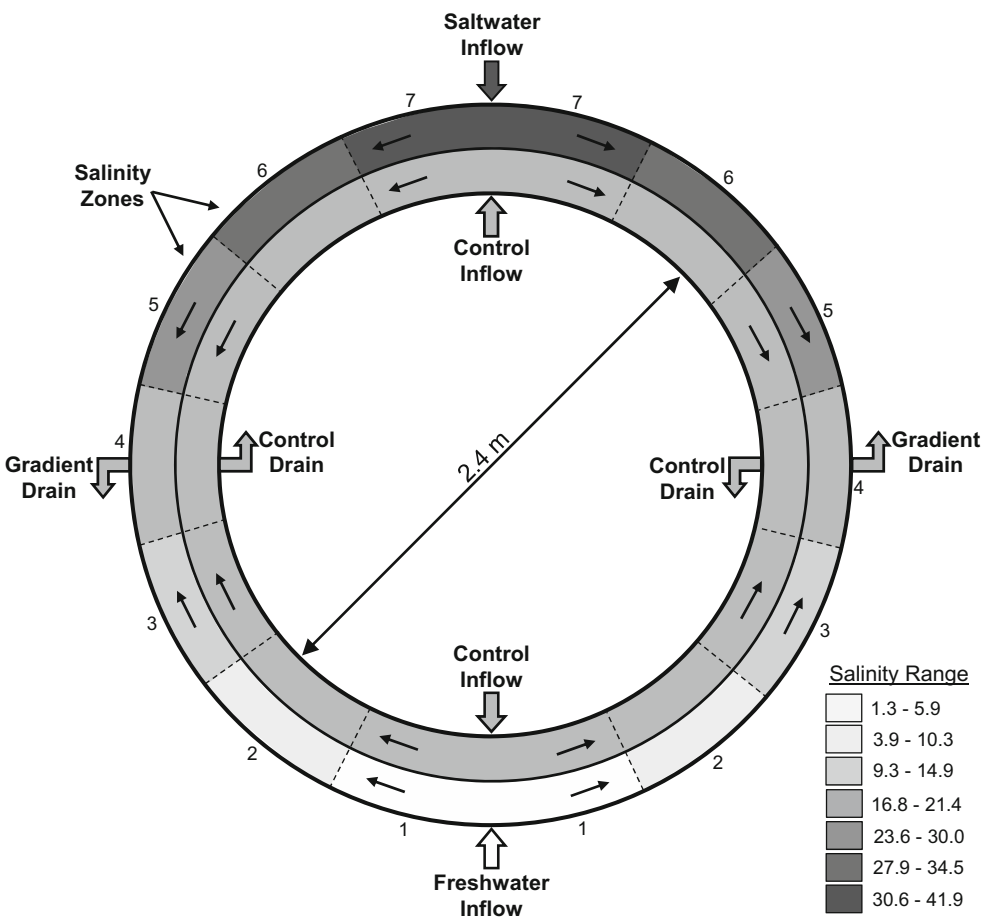

Fig. 2 Schematic representation of the gradient tank from an overhead view. In this configuration, the salinity gradient is in the outer (experimental) raceway and the control is in the inner raceway. *Arrows* show the direction of water flow; the width of each raceway is 0.15 m. The salinity ranges for each salinity zone listed in the legend are those from the brown shrimp trials. *Dashed lines* illustrate the conceptual boundaries of the seven salinity zones used to calculate mean salinities and record shrimp counts used in the contingency table and log-linear modeling analyses

Freshwater was obtained from city tap water filtered through a commercial dechlorinator unit, which removed chlorine and other freely associated ions via an activated charcoal filter. Commercial sea salts were mixed into the dechlorinated tap water until fully dissolved, and the salinity was 45 (Fritz Industries, Mesquite, TX). This approach was designed to avoid confounding salinity effects with other characteristics of natural sea water.

The gradient raceway actually contained two salinity gradients (each 4.25 m in length) that extended in a semicircle from one water input to the other (Fig. 2). In an earlier design, we created a similar gradient in a long horizontal tank with inputs on each end and a drain in the center, but shrimp in this system were attracted to the ends of the tank. The circular design used in this study eliminates that problem. The steepness of the salinity gradient in the chamber is readily controlled by adjusting the rates of water inflow.

Juvenile shrimp were collected throughout the year using seines in Galveston Bay, TX. In the lab, shrimp were separated according to species and collection date and held in recirculating tank systems (3785-L capacity) filled with artificial saltwater at a salinity of 20 and ambient room temperature. Shrimp were held for a minimum of 48 h prior to an experiment to ensure recovery from handling stress following capture. During holding, shrimp were fed daily with commercial shrimp production pellets (Rangen, Inc., Angleton, TX).

Prior to beginning a trial, both the experimental and control raceways were filled to 10 cm in depth with artificial saltwater at a salinity of 20 and ambient room temperature. To start a trial, 50 juvenile shrimp were distributed evenly in each raceway and allowed to acclimate for 30 min before the supply water inputs were turned on. Flow rates necessary to establish and maintain the gradient were 3.4 L min^{-1} of freshwater and 2.4 L min^{-1} of saltwater. At these input rates, the average water flow in the raceway was between 16 and 23 cm min^{-1}. The flows in the control raceway (salinity of 20) were adjusted to match the input rates in the experimental raceway. We measured salinity in the experimental raceway every hour at multiple locations using a pipette and a temperature-compensated refractometer to examine the stability of the gradient. The amount of water available in the supply tanks limited the duration of the trials to 7 h, and we recorded the distribution of shrimp in both raceways at the conclusion of each trial. Counting of shrimp was facilitated by lowering plastic mesh screens that isolated shrimp at their respective locations in the raceways.

We conducted 12 brown shrimp trials and seven white shrimp trials. Shrimp size was determined by availability in the estuary and ranged from 30- to 75-mm total length. All trials were performed under overhead fluorescent lighting supplemented by hanging pendant fixtures to ensure even illumination across the tank (range=28–33 lux). In some trials, the experimental and control raceways and the freshwater and saltwater inputs were interchanged to eliminate the possibility that features of the tank design or external laboratory characteristics could affect our results.

We conducted a frequency analysis on categorical data to explore the associations between shrimp counts in the experimental (varying salinity) and control raceways (constant salinity of 20) and salinity. In this analysis, we assumed that any artifacts from the tank, flow rate, or experimental setup that might affect shrimp distributions would be trivial and constant between raceways. Based on the observed distribution of salinities in the experimental raceway, we grouped the salinity measurements and shrimp counts into seven equal salinity zones for analysis, and we compared the difference in shrimp counts between the experimental and control raceways in these seven zones. Replicate trials on different days were treated as independent observations, and shrimp counts were pooled together for subsequent statistical analyses. This resulted in a 2×7 contingency table between two categorical variables: treatment (two levels, experimental and control) and salinity (seven levels). We tested the homogeneity of shrimp counts between the experimental and control raceways using Fisher's exact test. Our null hypothesis was that salinity would not affect shrimp distributions, and significant inconsistency would be evidence of salinity selection occurring during the trials.

We then conducted log-linear modeling analyses to examine relationships with salinity in more detail and to assess possible interactions between salinity selection and temperature (Quinn and Keough 2002). A log-linear model is a generalized linear model applied to count data, and these methods can be used to model cell counts in contingency tables and examine the relationships among variables in multi-way tables. The models formulate how the size of a cell count depends on the levels of the categorical variables for that cell (Agresti 1996; Anderson 2008). The water temperature in the experimental and control raceways was constant for each trial, but the overall ambient water temperature varied among the independent brown shrimp trials from 25 to 31 °C and among white shrimp trials from 23 to 31 °C. In the log-linear modeling analyses, we designated temperature as a categorical variable with six levels (25, 27, 28, 29, 30, 31 °C) for brown shrimp and four levels (23, 26, 30, 31 °C) for white shrimp.

The fully saturated log-linear model representing our three categorical variables of treatment (TRT, experimental versus control), salinity (SAL), and temperature (TEMP) and all possible interactions in a three-way contingency table would look like:

$$\ln\left(y_{ijk}\right) = \hat{\lambda} + \hat{\lambda}_i^{\mathrm{TRT}} + \hat{\lambda}_j^{\mathrm{SAL}} + \hat{\lambda}_k^{\mathrm{TEMP}} + \hat{\lambda}_{ij}^{\mathrm{TRT}\times\mathrm{SAL}} + \hat{\lambda}_{ik}^{\mathrm{TRT}\times\mathrm{TEMP}} + \hat{\lambda}_{jk}^{\mathrm{SAL}\times\mathrm{TEMP}} + \hat{\lambda}_{ijk}^{\mathrm{TRT}\times\mathrm{SAL}\times\mathrm{TEMP}}$$

Here, y represents the cell counts of shrimp and the subscripts i, j, and k refer to the categories within each categorical variable. $\hat{\lambda}$ is the parameter for the intercept-only model, $\hat{\lambda}_i^{\mathrm{TRT}}$, $\hat{\lambda}_j^{\mathrm{SAL}}$, and $\hat{\lambda}_k^{\mathrm{TEMP}}$ are the main effects reflecting the differences in marginal counts for the categorical variables of treatment, salinity, and temperature. The interaction terms are represented by $\hat{\lambda}_{ij}^{\mathrm{TRT\times SAL}}$, $\hat{\lambda}_{ik}^{\mathrm{TRT\times TEMP}}$, $\hat{\lambda}_{jk}^{\mathrm{SAL\times TEMP}}$, and $\hat{\lambda}_{ijk}^{\mathrm{TRT\times SAL\times TEMP}}$ and refer to a specific departure from independence. For example, in generic terms, the parameter $\hat{\lambda}_{ij}^{\mathrm{A\times B}}$ represents a difference in the observed counts from the independence model whereby the probability of observations falling into categories defined by B differs across categories defined by A. The null model for the three-way contingency table takes the following form:

$$\ln\left(y_{ijk}\right) = \hat{\lambda} + \hat{\lambda}_i^{\mathrm{TRT}} + \hat{\lambda}_j^{\mathrm{SAL}} + \hat{\lambda}_k^{\mathrm{TEMP}}$$

Log-linear models are useful for detecting association patterns among a set of categorical variables and investigating specific hypotheses related to interactions among confounding variables (Agresti 1996). Specifically, if the interaction terms among specific categorical variables were removed and the log-linear model still fits the observed frequencies adequately, we can conclude that the two variables are unrelated. Therefore, log-linear modeling analysis allowed us to tease apart the potential interactive effects from temperature on the relationship between salinity and counts in experimental and control raceways. In our analysis, the saturated model included the variables TRT, SAL, and TEMP and all of the interactions among these terms. Some interactions are of little interest, difficult to interpret, and possibly artifacts of the experimental design, so we focused on examining the null model shown above combined with interactions between TEMP and the TRT × SAL interaction:

$$\ln\left(y_{ijk}\right) = \hat{\lambda} + \hat{\lambda}_i^{\mathrm{TRT}} + \hat{\lambda}_j^{\mathrm{SAL}} + \hat{\lambda}_k^{\mathrm{TEMP}} + \hat{\lambda}_{ij}^{\mathrm{TRT\times SAL}}$$

We compared these models using Akaike's information criterion (AIC) and advanced AICc, which corrects for degrees of freedom in the model (Anderson 2008). We also examined residuals and performed likelihood ratio (LR) tests to evaluate whether the selected models adequately fit the observed frequencies. Note that non-significant p values (>0.05) for the LR tests indicate that models are not significantly different from the saturated model and suggest that the models with reduced factors can adequately explain variability in cell frequencies. Statistical analyses were conducted in R (R Project for Statistical Computing, version 2.13.2).

Results

The salinity gradient in the experimental raceway developed quickly (approximately 15 min) and remained relatively stable for the duration of the trial. Minor adjustments to flow rates were performed in some trials to maintain gradient stability. Shrimp exhibited increased and erratic movements when introduced into the tank but resumed apparent normal activity levels within approximately 30 min. Shrimp that were actively swimming moved in both directions around the tank, suggesting that their movement was not influenced by water flow inside the raceways. For all brown shrimp experiments, the salinity in the experimental raceway ranged from a minimum of 1 to a maximum of 42 ($\bar{x}_{\mathrm{Zone\ 1}} = 3.3$, $\bar{x}_{\mathrm{Zone\ 7}} = 36.7$, Table 1). Experiments with white shrimp had a minimum salinity of 2 to a maximum of 35 in the experimental raceway ($\bar{x}_{\mathrm{Zone\ 1}} = 4.8$, $\bar{x}_{\mathrm{Zone\ 7}} = 33.0$).

For brown shrimp, the analysis of homogeneity for the 2×7 contingency table indicated a significantly different pattern between the experimental and control raceways in relation to salinity (Table 2, Fisher's exact test, p=0.00001, df=6). Brown shrimp in the salinity gradient appeared to avoid low salinities (1.3–14.9) but selected for salinities between 16.8 and 34.5 (Fig. 3), and there was no effect of water temperature on the observed distribution. The log-linear modeling analysis for brown shrimp included three factors (TRT, SAL, and TEMP) in a 2×7×6 contingency table, and the residual deviance and LR test supported model 3 (Table 3). Model 3 had the lowest AICc and indicated significant interactions between treatment (the experimental raceway) and salinity selection in our experiments.

Table 1 Salinity measurements for designated salinity zones of the experimental raceway used in the contingency table and log-linear modeling analyses

	Brown shrimp				White shrimp				
Salinity zone	*N*	Mean	Min	Max	*N*	Mean	Min	Max	SE
1	144	3.3	1.3	5.9	84	4.8	2.3	9.9	0.90
2	144	7.0	3.9	10.3	84	9.1	7.6	14.5	0.91
3	144	12.2	9.3	14.9	84	13.2	11.0	18.3	0.86
4	144	19.5	16.8	21.4	84	19.0	16.9	23.6	0.88
5	144	26.6	23.6	30.0	84	24.8	22.9	28.0	0.66
6	144	32.3	27.9	34.5	84	29.9	28.1	31.9	0.57
7	144	36.7	30.6	41.9	84	33.0	30.5	35.0	0.57

Shown are the mean, minimum, and maximum salinity values (plus 1 standard error (SE)) recorded across all brown and white shrimp salinity trials. Salinity values shown were calculated from measurements collected during the final observational period of each trial. The range of salinity in individual salinity zones during the trials was determined from salinity measurements taken at 12 locations within each salinity zone

Table 2 Contingency table for brown shrimp selection experiments testing for independence of shrimp counts between experimental raceway (varying salinity) and control raceway (constant salinity of 20)

Salinity zone								
	1	2	3	4	5	6	7	Total
Control	95	64	70	78	76	89	119	591
Experimental	46	55	56	121	96	116	95	585
Total	141	119	126	199	172	205	214	1176

Data are total counts from 12 independent experimental trials. Fisher's exact test for treatment with simulated p value=0.00001, df=6

The distribution of juvenile white shrimp in the gradient tank varied with no apparent selection for salinity (Fig. 4), and the test for homogeneity based on the 2×7 contingency analysis (Table 4) indicated that there was no significant pattern between counts in the experimental raceway with varying salinity versus that in the control raceway with constant salinity (Fisher's exact test, p=0.084, df=6). The lack of significance in this 2×7 contingency table for white shrimp may have been partly due to the lower number of trials conducted for this species (seven) compared with brown shrimp (12 trials). The most parsimonious log-linear model was the null model (Table 5, model 2), indicating that there was no significant interaction among the three categorical variables in the 2×7×4 (TRT × SAL × TEMP) contingency table for white shrimp.

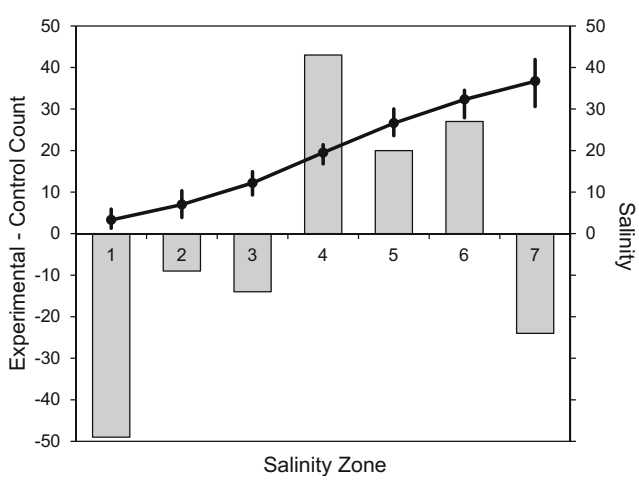

Fig. 3 Relationship between the difference in juvenile brown shrimp counts between the experimental and control raceways (column values indicated by the count scale on the *left axis*). Values near zero indicate no salinity preference; positive values indicate selection for a particular salinity zone, and negative values indicate avoidance. Also shown are the mean salinity values for each zone (*closed circles*) and the range of salinities (*vertical bars*) recorded in each salinity zone of the experimental raceway during the 12 trials (values correspond to the salinity scale on the *right axis*)

Discussion

The abundance of juvenile penaeid shrimp in estuarine systems is influenced by a combination of physical and environmental characteristics, and the conflicting reports of relationships between abundance and salinity in the literature likely reflect this complexity (Longley 1994; Minello 1999). Efforts to determine whether salinity is an important driver of shrimp distributions mainly have been limited to field capture and empirical studies, with few experimental investigations in the field or in the laboratory. Laboratory gradient studies can add to our understanding of the role that salinity plays in shrimp distributions, because these experiments provide shrimp with the opportunity to actively choose among available salinities. However, technical difficulties have limited the use of this experimental approach which requires the establishment of stable gradients without other associated factors that might influence distributions. The circular raceway design described here eliminates many technical barriers and allows an examination of selection along a gradient with salinities from 1 to 42 over a raceway length of approximately 8.5 m.

Juvenile brown shrimp in our gradient trials generally selected for salinities in the range of 17 to 35 and against lower salinities and extreme high salinities. We did not observe a relationship between water temperature and salinity selection in our experiments, but Howe et al. (1982) reported that both brown and white shrimp displayed an increased sensitivity to high salt concentrations in river water brine at 30 °C. Other experiments on postlarval brown shrimp growth and survival suggest a physiological response between temperature extremes and salinity. For example, maximum growth of postlarval (mean total length 12.1 mm) brown shrimp occurred at salinities of 25 and 32 °C; however, survival decreased at temperatures greater than 25 °C regardless of salinity, and total mortality occurred above 35 °C (Zein-Eldin and Aldrich 1965; Zein-Eldin and Griffith 1966).

Juvenile white shrimp in our gradient trials were generally more abundant in lower salinities than brown shrimp (below 18), but our sample size was low, and these results were not statistically significant. In their slanted tank, Keiser and Aldrich (1976) reported that postlarval white shrimp selected for salinities in the range of 13–28, with a mean preference at 15. Although our ambient water temperature varied from 23 to 31 °C between trials, we found no evidence to suggest that water temperature affected salinity selection of juvenile white shrimp. Laboratory studies showed that highest growth rates for this species (postlarvae at 6.1-mm total length) occurred in salinities from 2 to 15 and 32 °C, with growth decreasing substantially between 18 and 25 °C (Zein-Eldin and Griffith 1969). White shrimp in these experiments were able to tolerate slightly higher temperatures than brown shrimp, with total mortality only occurring above 37.5 °C (Zein-Eldin and Griffith 1969).

Table 3 Log-linear model results for brown shrimp to examine the potential interactions among the three categorical variables of treatment, salinity, and temperature in a 2×7×6 contingency table

Model	Effects	AIC	AICc	Residual deviance	Residual *df*	LR test (*p* value)
Model 1 (saturated)	TRT, SAL, TEMP, and all interactions	936.9	1109.0	156.3	84	<0.0001
Model 2	TRT, SAL, TEMP	908.8	911.2	172.9	155	0.1551
Model 3	TRT, SAL, TRT × SAL	888.9	891.6	172.2	154	0.1506
Model 4	TRT, SAL, TRT × TEMP	935.5	937.5	173.5	156	0.1600
Model 5	TRT, SAL, TEMP, TRT × SAL × TEMP	936.9	1108.9	156.3	84	<0.0001
Model 6	TRT, TEMP	925.6	926.3	173.5	161	0.2366
Model 7	TRT, SAL	899.0	899.9	172.8	160	0.2314
Model 8	SAL, TEMP	906.9	908.9	173.1	156	0.1659

External factors such as the salinity and temperature of the water in holding systems or length of time in captivity have been reported to affect salinity selection by marine organisms in other laboratory experiments (Forward 1989; Keiser and Aldrich 1976; Miller et al. 1983). All shrimp in our holding systems were acclimated to a salinity of 20, a commonly recorded salinity in Galveston Bay estuaries where the experimental shrimp were collected. Our log-linear modeling analyses showed that there was no apparent relationship between water temperature and the distribution of brown shrimp or white shrimp in our salinity gradient experiments.

While size may be a factor in salinity selection, this aspect was not assessed in the present analysis to focus on temperature and salinity effects. In experiments with different species of penaeids, Mair (1980) reported that older and larger postlarval shrimp preferred lower salinities and were also able to adapt to lower salinities more quickly than smaller shrimp. Zein-Eldin and Aldrich (1965) found the opposite and suggested that postlarvae were better osmoregulators than larger shrimp and thus were more tolerant of a wider salinity range. Keiser and Aldrich (1976) found that smaller postlarvae generally preferred higher salinities than did the larger shrimp, but that salinity preference by age was also variable for both brown shrimp and white shrimp. The shrimp in our study ranged from 30- to 75-mm total length and should be representative of most juveniles found in Gulf estuaries. Salinity preferences for larger subadults as they prepare to leave estuaries or for adults offshore may differ from the juveniles that we studied.

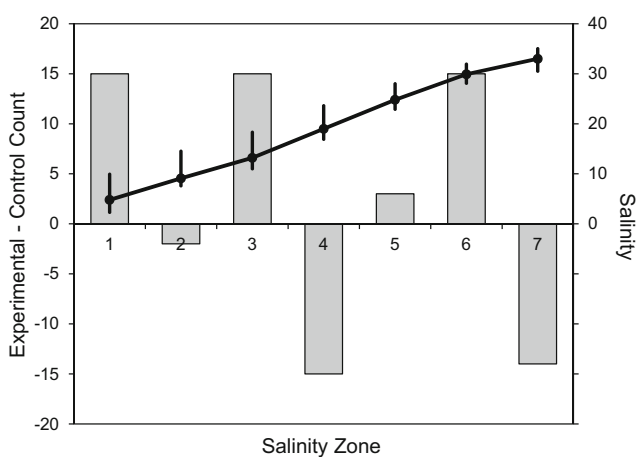

Fig. 4 Relationship between the difference in juvenile white shrimp counts between the experimental and control raceways (column values indicated by the count scale on the *left axis*). Values near zero indicate no salinity preference; positive values indicate selection for a particular salinity zone, and negative values indicate avoidance. Also shown are the mean salinity values for each zone (*closed circles*) and the range of salinities (*vertical bars*) recorded in each salinity zone of the experimental raceway during the seven trials (values correspond to the salinity scale on the *right axis*)

The broad range of salinities selected by brown shrimp and the lack of a salinity selection pattern by white shrimp in our laboratory experiments suggest that moderate variations in salinity do not drive distributions of these species in estuaries. These results might generally explain the highly variable field distributions reported for brown shrimp and white shrimp in relation to estuarine salinity (see Adamack et al. 2012; Rozas and Minello 2010 for reviews). Apparent relationships between shrimp abundance and salinity may be caused by interactions with other environmental factors such as water temperature or with secondary and related factors such as the abundance of benthic infaunal food (Rozas and Minello 2011).

The effect of salinity on shrimp production has been examined through studies on growth and survival. Zein-Eldin

Table 4 Contingency table for white shrimp selection experiments testing for independence of shrimp counts between experimental raceway (varying salinity) and control raceway (constant salinity of 20)

Salinity zone								
	1	2	3	4	5	6	7	Total
Control	42	39	34	71	41	32	60	319
Experimental	57	37	49	56	44	47	46	336
TOTAL	99	76	83	127	85	79	106	655

Data are total counts from seven independent experimental trials. Fisher's exact test for treatment with simulated *p* value=0.084, *df*=6

Table 5 Log-linear model results for white shrimp to examine the potential interactions among the three categorical variables of treatment, salinity, and temperature in a 2×7×4 contingency table

Model	Effects	AIC	AICc	Residual deviance	Residual *df*	LR test (*p* value)
Model 1 (saturated)	TRT, SAL, TEMP, and all interactions	536.7	692.4	74.4	42	0.0015
Model 2	TRT, SAL, TEMP	528.2	531.3	115.6	87	0.0218
Model 3	TRT, SAL, TRT × SAL	526.9	532.0	117.3	84	0.0097
Model 4	TRT, SAL, TRT × TEMP	534.4	536.0	113.7	90	0.0467
Model 5	TRT, SAL, TEMP, TRT × SAL × TEMP	536.7	692.4	74.4	42	0.0015
Model 6	TRT, TEMP	528.7	529.3	113.6	93	0.0720
Model 7	TRT, SAL	522.5	524.2	115.6	90	0.0359
Model 8	SAL, TEMP	526.6	529.2	115.8	88	0.0251

(1963) and Zein-Eldin and Aldrich (1965) concluded that only extreme salinity conditions significantly affected growth and survival of brown shrimp postlarvae. Survival of postlarvae decreased in salinities less than 5 when temperatures were below 15 °C (Zein-Eldin and Aldrich 1965). Saoud and Davis (2003) reported growth of juvenile brown shrimp to be considerably higher at salinities of 8 and 12 compared with 2 and 4. Postlarval white shrimp exhibited maximum growth rates in salinities from 5 to 15 in laboratory experiments (Zein-Eldin and Griffith 1969). Similar to brown shrimp, the survival rate of postlarval white shrimp at salinities of 25 decreased with decreasing temperatures, with complete mortality at a low temperature threshold of 7.5 °C (Zein-Eldin and Griffith 1969). In field growth experiments on both juvenile brown shrimp and white shrimp, reduced growth at low salinities was attributed to the combined effects of increased metabolic costs and a reduction in available food sources (Rozas and Minello 2011, 2015). This effect of salinity on benthic infaunal food and growth of brown shrimp was examined in more detail and modeled by Adamack et al. (2012).

Other modeling studies also support a relationship between salinity and brown shrimp production. Using a model developed in North Carolina, Hunt et al. (1980) identified a threshold of 10 as the lowest salinity supporting a good commercial brown shrimp harvest. In Louisiana, Barrett and Gillespie (1973) concluded that salinities above 19 in April and May were optimum for brown shrimp production in the estuary. Haas et al. (2001) compiled long-term monitoring data from Louisiana and determined that salinity was not a reliable predictor for the abundance of postlarval brown shrimp, but that abundance of adult brown shrimp was positively correlated with increased salinity in the estuary.

Understanding the relationships between salinity and distributions of juvenile penaeid shrimp in estuarine systems is particularly important for evaluating impacts of anthropogenic changes to freshwater inflow. Freshwater diversions are used widely in Louisiana to combat land loss and restore coastal wetlands (Day et al. 2009; Piazza and La Peyre 2011). Incoming river water is usually cooler than estuarine waters and can reduce salinities in entire estuaries to freshwater levels for short periods of time (Day et al. 2009). Since brown shrimp recruit to estuaries in the spring, increases in freshwater inputs could potentially reduce growth rates via decreased water temperature and salinity. The results of our experiments suggest that white shrimp may be more likely to remain in the estuary during extreme freshwater events, while brown shrimp may shift their distribution and relocate to higher salinity regions of the estuary.

Our salinity gradient tank has some advantages over related designs for examining salinity selection by mobile marine organisms. The tank design allows for simultaneous testing of experimental and control animals under similar conditions. The experimental and control raceways also can be alternated during subsequent runs. We were able to eliminate structural components, such as physical barriers and discontinuity layers, from previous designs that may inadvertently influence apparent salinity selection. However, some of the variability in our results was likely caused by characteristics of the experimental system. Water temperature did not appear to affect salinity selection in our experiments, but differences caused by seasonal fluctuations can confound the interpretation of selection patterns. Overhead lighting in our experiments was supplied by fluorescent bulbs, but ensuring consistent illumination and eliminating shadows within the raceways proved difficult, and variations in light can affect shrimp behavior. In addition, some variability may have been introduced by fluctuations in the gradient, in particular, the intricacies involved in establishing and maintaining extreme salinities at either end of the gradient. Also, because this is a flow-through system, the duration of an individual experiment was limited by the amount of prepared freshwater and saltwater available in the supply tanks. Despite these caveats, this circular raceway design provides a useful method to examine nekton selection within a gradient, with the potential to examine gradients in temperature and turbidity as well as salinity.

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